



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE AMERICAN NATURALIST.

VOL. XV. — *FEBRUARY*, 1881. — No. 2.

INCOMPLETE ADAPTATION AS ILLUSTRATED BY THE HISTORY OF SEX IN PLANTS.¹

BY LESTER F. WARD, A.M.

THE doctrine of abrupt changes or cataclysms in nature has a remarkable survival in the still prevalent belief in perfect adaptation. As it was formerly held that organisms were purposely made for their conditions and exactly adjusted to them, so now, since the law of self-adjustment has become current, it is supposed that the organism and the environment have in all cases reached a condition of complete correspondence. It is in virtue of this assumption that the law of cross-fertilization of plants has been called in question, and an eminent botanist once remarked to me that the slight difference between the results of Darwin's experiments under cross and under self-fertilization, amounting on an average to one-fifth of the whole, was sufficient to invalidate that law.

Nothing seems so difficult for the human mind to grasp as change through minute variations indefinitely continued. Even those who admit that this is nature's method, fail to realize it in concrete examples.

We may suppose that a given character not possessed by a given species would, as a matter of fact, be an advantage to such species if it could acquire it. We may further suppose that for any reason the species commences to vary in the direction of acquiring that character. The benefit will be proportional to the degree of completeness with which the character is attained.

¹ Read before the Biological Section of the American Association for the Advancement of Science, at Boston, August 27, 1880.

Under the law of natural selection, the perfection of the character will ultimately be reached, but a very long period, to say the least, must elapse during which it is still incomplete.

Again, the conditions surrounding a species are constantly changing, usually slowly, but sometimes rapidly or suddenly. In this way the usefulness of certain characters is frequently destroyed, but the species cannot lose the character; it persists and gradually becomes atrophied or transformed into a different one. Such changes in organisms are very slow, and vast periods are passed through before they are completed.

Now, considering the changes going on at all times in the conditions under which species exist, it may often happen that the period during which adaptation is incomplete from both these causes, is greater than that during which it is complete. Indeed, as a matter of fact, the adaptation is never absolutely complete, the organism being always, as it were, behind its environment, as the tides are behind the moon.

If this be true, we ought to expect constantly to find examples of incomplete adaptation. A character which required to be complete before it could be advantageous could never be acquired by natural selection. All such characters as are acquired must be advantageous in proportion as they are complete.

Naturalists must therefore learn to regard a large proportion of the characters which they find to exist, as partial or uncompleted characters, useful to the species in proportion as they are developed, but capable of greater adaptation.

There are, moreover, two general classes of characters with respect to their usefulness and advantageousness to the species. Those of one of these classes are only useful to a certain limited degree, beyond which they may be injurious, and which only apply to particular species in their relations to definite existing conditions. Such characters may be called *special*.

The other class, which may be distinguished as *general*, apply to all organisms, and are less limited in their degrees of possible development.

Passing over the class of special characters, I propose to illustrate the principles above stated, by an example in the class of general characters taken from the vegetable kingdom.

The distinction of sex is a condition advantageous to all plants, and one in the process of attaining which a large number of grada-

tions are to be found. The purely asexual state exists only in the lowest Protophytes, as in *Saccharomyces*, the *Phycochromaceæ*, and other unicellular forms. The simple phenomenon of conjugation or copulation seen in the *Zygomycetæ* and diatoms, forms the earliest step towards sexual differentiation, which is followed by the various intermediate steps represented by the pairing of active cells in *Volvox*, the formation of oöspores in the *Confervæ* and *Fucaceæ*, and of carpospores in the *Fungi*.

In the *Characeæ* we first find the well marked distinction of antheridia and carpogonia, the former furnishing in *Nitella* the active spermatozooids which differ immensely from the cells with which they combine. This latter feature continues to characterize all the higher Cryptogams, though in nearly all cases the organs of both sexes are borne on the same plant. The transition from the Cryptogams to the Phanerogams is effected by a primary differentiation of the spores, which in most Cryptogams are the independent asexual bodies that produce the sexually differentiated prothallium. This prothallium loses its independence and becomes the albumen of the seed; the male spores are converted into pollen grains and the antheridia into the fertilizing pollentubes; the female spores are transformed into embryo-sacs containing corpuscles within which are the ultimate germ-cells.

In a certain sense this transition, instead of marking an advance in the process of sexual separation, constitutes a step backward, since the prothallia of Cryptogams, considered as distinct individuals, are respectively male and female, while the stamens and pistils of the *Cycadaceæ* and *Coniferæ*, the earliest Phænogams developed, though quite distinct in themselves, are both borne on the same plant. But the prothallium marks the highest development reached or possible to the Cryptogam. The Phænogam must begin from a point lower down, and in turn evolve sexually differentiated forms. The distinction of macrospores and microspores found only in the *Rhizocarpeæ* and *Ligulatæ*, and which, as already stated, initiated the transition from the Cryptogams to the Phænogams, took place in the same individual, both kinds of spores often occurring in the same sporangium, as in *Salvinia*. This, when the two kinds of spores at length came to represent the two sexual organs of the Cycad or the Conifer, necessarily reunited the sexes once more in the same plant, and the process of separation, so well completed in the higher Crypto-

gams, was required to be begun anew on the higher Phænogamic plane of development.

From this point, however, the history of this process is of the highest interest. In the Cycadaceæ complete diœcism was reached before any of the few now existing forms were developed, and all present living species are male and female. In the Coniferæ, different families have attained to different degrees of diclinism. The Taxineæ, which many facts show to have been among the earliest forms developed, are diœcious, while the great pine and fir tribes, as well as most cedars, are still monœcious. Both these great orders have come down to us from the Carboniferous epoch, and indicate, along with the remnant which we possess of the then luxuriant cryptogamic flora, the kind of vegetation which prevailed in those remote ages. The flowers even of the highest forms were uniformly inconspicuous and odorless. The only possible substitute for sexual separation was the distribution of pollen by the winds. Forms so high in development, it would seem, could not continue to exist through self-fertilization alone, and hence, under the operation of natural selection, more or less complete sexual separation early took place.

The transition from the Gymnosperm to the Angiosperm is veiled in great obscurity. Certain considerations point to the gradual transformation of the Cycadaceæ into the Monocotylæ through the Palmaceæ or some allied family, on the one hand, and to that of the Coniferæ into the Dicotylæ through the Gneta-ceæ and Casuarineæ, on the other. However this may be, the earliest known fossil species of Angiosperms, dating back to the early Trias, consist of poplars, beech, oak, chestnut, sycamore, and other unisexual and diœcious trees, all of which want the showy flowers characteristic of the present flora of the globe.

In view of the fact that this early flora was to so great an extent diclinous, it becomes an important question why so large a proportion of the present flora is hermaphrodite. We find that many of the plants of the most recent geological development possess the means of self-fertilization within the same flower and no obvious means of crossing individuals. Upon closer observation, however, we perceive that many of these apparently perfect flowers possess arrangements of a more or less anomalous kind, which, inexplicable on any other theory, are all explainable as contrivances for the prevention of self-fertilization. The com-

pleteness with which this object is accomplished is of all degrees, from *Epilobium* with its style merely turned to one side, to *Iris* with its short extrorse anthers hidden away under the broad styles stigmatic on the inaccessible side; from mere heterostyly to complete dichogamy.

I need not review the conclusive reasoning by which all these morphological modifications are accounted for as the results of the long continued agency of insects. It is important only to point out that this influence has been powerful enough to reverse the entire course of sexual differentiation, which, as we have seen, has been in all lower forms constantly in the direction of a more and more complete separation of the sexes. It may be said that this proves too much, since progress in that advantageous direction once gained would not be likely to be lost. The sufficient reply to this is that, independently of the natural tendency to revert to the normal or monosexual state, when the separative influences are withdrawn, the reserve power of possible self-fertilization when for any cause cross-fertilization fails, as it clearly often may, is a positive advantage, and one which, under the proper circumstances, natural selection will insure.

The most significant fact which palæontology reveals is that of the simultaneous appearance of an insect fauna and a hermaphrodite flora. When the insects came upon the scene they found only a diclinous flora with usually apetalous flowers destitute of both fragrance and color. The succeeding strata immediately commence to exhibit plants of the rose, mallow, magnolia, pulse, and crowfoot families with showy petals, often fragrant, and provided with special nectaries for the secretion of honey. Most of these had already made their appearance in the chalk formation, while during the Tertiary the still more perfectly organized Gamopetalæ were developed. The agency of insects in the fertilization of plants and even in the transformation of flowers to adapt them to their uses is no longer questioned by any at all familiar with the facts, but wide differences of opinion exist with regard to the degree of this influence, and also to the meaning of particular facts. Much of this confusion is due to the prevalence of the notion to which attention was called at the outset, that all adaptation must be regarded as completed at the present time. This assumption of a statical condition in nature now, while admitting the necessity of a dynamical condition in the past, is

wholly gratuitous and belongs, as already remarked, to the same class of ideas as that by which all changes were once explained as the results of great and sudden catastrophes. It is due to the kind of reasoning which denies change to everything which can not be seen to move—a kind of reasoning which leads the savage to deny that the great trees have ever been other than they are,¹ while admitting growth in the herb and the sapling. In point of fact we find nearly all possible degrees of adaptation to the agency of insects. The mere existence of colored flowers must be regarded as an initial step in this direction, and the greater part of all flowering plants exhibit in a more or less marked manner this evidence of the influence which insects have exerted upon them. But it is evident that an ordinary hermaphrodite flower, however showy or fragrant, if devoid of special appliances for preventing self- and securing cross-fertilization, represents a very rudimentary and imperfect state of correlation to the insect world. This condition, which is now the predominant one, must therefore be regarded as constituting the first step of a long progressive series of morphological changes in the same direction, all tending to complete the degree of adaptation to insect life. The various specializations which a few species have already undergone mark so many additional steps taken by such species toward the same end and afford a faint idea of what the whole flora of the globe might become in the remote future, if wholly uninfluenced by man.

In the great majority of plants, self-fertilization is doubtless still the rule, and cross-fertilization the exception, but this occasional crossing, even though very rare, suffices to maintain the vigor of the stock. Such plants will appear to thrive as well when self-fertilized as when cross-fertilized, and this would probably be the case if the experiment were repeated a great number of times, for it is not once or a score of times, or a hundred times even, that count in these processes of nature, but vast periods and innumerable repetitions, each with its minute differential to add to or subtract from the general sum. When these facts are properly understood, therefore, the partial or total failure of all human experiments on cross-fertilization becomes nothing more than naturalists ought to expect. The really surprising fact in such

¹ See an address by Maj. J. W. Powell, delivered before the American Geographical Society, at Chickering Hall, New York, Dec. 29th, 1876.

experiments is that some of them actually do show a clear difference in favor of cross-fertilization. It may be compared to the attempt of astronomers to obtain the parallax of a fixed star. The result is in the highest degree satisfactory if it is certain that any positive angle is measured. And, as in the astronomical parallax, the greatest exactness is required to measure the vastness of space and its contents, so in the biological parallax equally great precision is needed to measure the vastness of time and its effects.

Independently of insect agency, however, the vegetable kingdom furnishes many facts which prove the unstable state in which the sexual relations are still found to exist.

In many cases it is difficult to determine whether the movement is at the present time towards a greater or a less degree of separation. In a former paper read before this Association¹ I endeavored to bring forward the evidence to prove that certain species of Lauraceæ, and notably the genera *Sassafras* and *Lindera*, had already passed through three different stages, of which traces are still left in the form of "rudiments" or obsolete organs. In this case the movement has obviously been towards more complete sexual separation. In the majority of other common cases, such as *Smilax*, *Ilex*, *Rumex*, *Rhus*, *Chamælrimum*, &c., where the rudiments of both stamens and pistils remain, though one or the other set is functionless and the plants are really diœcious, the direction of development seems also to be towards sexual distinctness, and it may well be doubted whether the flowers of the oak, the alder, or the willow were ever hermaphrodite. Still, progress toward hermaphroditism may also be going on in some species where insect fertilization is found a sufficient substitute for the distinction of sex.

Upon the whole, however, it must be concluded that the special effect of the appearance of insects in the Mesozoic or Secondary age of geology was to render the evolution of new hermaphrodite forms possible, which vastly enriched the world's flora, since prior to that time only diclinous species could survive, and that this great army of plants, having been thus brought into existence in this imperfect condition, have since been gradually throwing off their encumbrance, and at different rates moving forward toward sexual independence.

¹ Published in the *Scientific American Supplement* of Sept. 20, 1879, p. 3089.